The fossil record of early tetrapods: Worker effort and the end-Permian mass extinction

EMMA L. BERNARD, MARCELLO RUTA, JAMES E. TARVER, and MICHAEL J. BENTON

Bernard, E.L., Ruta, M., Tarver, J.E., and Benton, M.J. 2010. The fossil record of early tetrapods: Worker effort and the end-Permian mass extinction. *Acta Palaeontologica Polonica* 55 (2): 229–239.

It is important to understand the quality of the fossil record of early tetrapods (Tetrapoda, minus Lissamphibia and Amniota) because of their key role in the transition of vertebrates from water to land, their dominance of terrestrial faunas for over 100 million years of the late Palaeozoic and early Mesozoic, and their variable fates during the end-Permian mass extinction. The first description of an early tetrapod dates back to 1824, and since then discoveries have occurred at a rather irregular pace, with peaks and troughs corresponding to some of the vicissitudes of human history through the past two centuries. As expected, the record is dominated by the well-sampled sedimentary basins of Europe and North America, but finds from other continents are increasing rapidly. Comparisons of snapshots of knowledge in 1900, 1950, and 2000 show that discovery of new species has changed the shape of the species-level diversification curve, contrary to earlier studies of family-level taxa. There is, however, little evidence that taxon counts relate to research effort (as counted by numbers of publications), and there are no biasing effects associated with differential study of different time intervals through the late Palaeozoic and Mesozoic. In fact, levels of effort are apparently not related to geological time, with no evidence that workers have spent more time on more recent parts of the record. In particular, the end-Permian mass extinction was investigated to determine whether diversity changes through that interval might reflect worker effort: it turns out that most records of early tetrapod taxa (when corrected for duration of geological series) occur in the Lower Triassic.

Key words: Discovery curve, collector curve, early tetrapods, fossil record, Tetrapoda, Temnospondyli, Lepospondyli, end-Permian mass extinction.

Emma Bernard [emma.bernard121@googlemail.com], Marcello Ruta [m.ruta@bristol.ac.uk], James E. Tarver [james.tarver@bristol.ac.uk], and Michael J. Benton (corresponding author) [mike.benton@bristol.ac.uk], Department of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, UK.

Received 10 February 2009, accepted 11 September 2009, available online 11 January 2010.

Introduction

The fossil record documents only a portion of extinct life. Therefore, it is important to determine where its incompleteness might lead to erroneous macroevolutionary conclusions (Smith 2007). An implicit assumption of most studies of past diversity has been that the quality of our knowledge of the fossil record is uniform through geological time. In other words, sampling is assumed to have been broadly constant through the history of any particular group, although with some improvement toward the present (Raup 1972). However, this implicit assumption of equal sampling is rarely tested, so many macroevolutionary studies must be regarded as suspect until such testing has been undertaken (Smith 2007).

Incompleteness of our knowledge of the fossil record may stem from both geological and human factors (Raup 1972). The term "sampling" is often used to reflect the interplay of these factors. Geological and biological reasons for poor sampling include absence of hard parts, under-representation of certain ecosystems, erosion, diagenesis, metamorphism, and subduction. Human factors include variable collecting and study of rocks and fossils of different geological ages, from different geographic regions, and from different facies, as well as varying modes of study and assumptions about species and genus demarcation.

One approach to understand how human factors affect sampling has been to examine how knowledge has accumulated through research time. For example, Maxwell and Benton (1990) and Sepkoski (1993) showed that accumulating knowledge of the fossil record of tetrapods and marine animals over the 100 and 10 years preceding their studies, respectively, had expanded the total numbers of taxa sampled, but that the broad macroevolutionary patterns had not changed substantially. In other words, palaeontologists have been adding new taxa more or less uniformly through the sampled geological time period, and the accumulation of new data has not modified apparent rises and falls in diversity. The study by Maxwell and Benton (1990) is germane to the present enquiry because they showed that numbers of tetrapod families had doubled from 1890 to 1987, and yet patterns of rises and falls in diversity through the Carboniferous to Triassic interval—

doi:10.4202/app.2009.0025

when early tetrapods composed most of the faunas—were little modified. This requires further assessment.

Uniformity of sampling is particularly important across mass extinction intervals. At worst, a postulated extinction crisis could be no more than a failure of sampling, perhaps resulting from the absence of suitable rock facies at a certain point (Smith 2007). Holland and Patzkowsky (1999) distinguished sampling bias (resulting from the rarity of species and the frequency and intensity of collection), facies bias (resulting from the facies sensitivity of different taxa), and unconformity bias (resulting from the wholesale removal or absence of rocks and fossils of particular ages).

The fossil record of continental tetrapods has been seen as much patchier, and perhaps less reliable than the record of marine invertebrates (e.g., Valentine 1969; Raup 1979; Benton 1985; Flessa 1990; Jablonski 1991). Studies of sampling (e.g., Maxwell and Benton 1990; Benton and Simms 1995; Benton 1996; Fara and Benton 2000; Fara 2002; Kalmar and Currie 2010) have confirmed both the presence of many gaps and the effect of the continuing accumulation of knowledge, but they have not highlighted any substantial differences from the outcomes of analogous studies of marine groups. Further, comparisons of stratigraphic and phylogenetic data (Norell and Novacek 1992; Benton and Storrs 1994; Benton et al. 2000) show that the fossil record of continental tetrapods is as good as that of marine invertebrates both in terms of completeness and in its ability to document the correct order of occurrence of groups, on the broad taxonomic and temporal scale (i.e., genera and families through stratigraphic stages and series).

We are interested in the extinction and survival of early tetrapods, and particularly the effect of the end-Permian mass extinction. Our focus here is on the accumulation of knowledge of "early tetrapods" (Tetrapoda minus Lissamphibia and Amniota) often loosely referred to as "amphibians") from their first occurrences in the Devonian through to the end of the Triassic. Jaeger (1824) reported the first pre-Jurassic tetrapod, the temnospondyl *Mastodonsaurus* from the Late Triassic of Germany, although the taxon was named officially only in 1828 (Jaeger 1828; see also Moser and Schoch 2007). Since then, new species have been reported in bursts, sometimes associated with individual researchers, or with the discovery of new deposits in the Carboniferous, Permian, and Triassic. In the past decades, discoveries have reflected scientific interest in macroevolutionary phenomena, with particular attention focusing on the origin of tetrapods, and the transition from the fish fin to the tetrapod limb: finds of tetrapods from the Devonian have doubled in the past 20 years (Clack 2002).

The pattern of accumulation of knowledge about any clade through research time may be documented by means of a collector curve (Cain 1938), also called a species accumulation curve (Gaidet et al. 2005) or a discovery curve (Wickström and Donoghue 2005; Bebber et al. 2007). We prefer the last term for studies such as this, where global species counts are being assessed. This technique was developed by ecologists who sought to determine the point at which they had collected enough specimens to compile a relatively complete species inventory of any area. In a collector curve, ecologists plot the number of new species identified against "effort", which might be days of searching or numbers of specimens collected/observed. In palaeontological examples (e.g., Benton 1998, 2008; Fountaine et al. 2005; Wickström and Donoghue 2005; Tarver et al. 2007), numbers of new genera or families identified are normally plotted against years in research time, the latter being a broad measure of effort.

The aims of this study are to determine (i) whether worker effort has varied through research time and so might affect the perception of the end-Permian mass extinction, and other macroevolutionary phenomena; and (ii) whether sampling has been affected by detectable "human" factors such as the country of origin of the fossils, events such as the world wars, and the termination of commercial coal mining.

Other abbreviations.—H, Kruskal-Wallis value; *p*, probabilty.

Materials and methods

Data.—The dataset includes all taxa referred to as "early amphibians" in the literature, namely all members of Tetrapoda, from the origin of the clade in the Late Devonian to the last temnospondyls in the Jurassic and Cretaceous, but excluding crown-group Amniota and Lissamphibia. Major clades included (Ruta et al. 2003) are Adelospondyli, Aïstopoda, Anthracosauria, Baphetidae, Colosteidae, Gephyrostegidae, Lysorophia, Microsauria, Nectridea, Seymouriamorpha, Temnospondyli, and Whatcheeriidae, as well as numerous Palaeozoic species that do not easily fit into any of the major groups (e.g., Devonian tetrapods).

For each group, a listing of all named species was made, including author and year of publication, as well as geographic and stratigraphic information. Geographic location was taken at least to the level of country or continent, with specific localities noted in most cases. Stratigraphic records were made to the level of the stage, where possible, based on cross-checking of the current age assignments of host formations; in a very few cases, particularly for older records, only a series could be determined. These cases (< 5% of the data) do not affect our study because we deal with all temporal questions in terms of stratigraphic series and systems. The raw data were compiled first from Carroll et al. (1998) on lepospondyls and Schoch and Milner (2000) on stereospondyls, and then updated from an intensive survey of more recent papers. Full details are given in the Supplementary Online Material (http: //app.pan.pl/SOM/app55-Bernard_etal_SOM.pdf) listing all early tetrapod species in order of the date of naming, with their authors, geological ages, geographic locations, together with calculations upon which Fig. 1 is based.

Synonymy and other false attributions of taxa can be a major source of error. This is as true for early tetrapods as for any other clade, and efforts were made to count only "currently valid taxa". Our plots then correspond to the

"valid now" category of Alroy (2002), and they do not include taxa that were once considered valid, his "valid then" category. The compendia noted include thorough reporting of synonyms, nomina nuda, nomina dubia, and other incorrectly named taxa. In the case of early tetrapods, many putative new genera and species have been established on incomplete specimens, and there have been phases of enthusiastic multiplication of taxa when numerous synonyms were generated. As an example, Moser and Schoch (2007) report more than 30 invalid species names for *Mastodonsaurus giganteus* (Jaeger, 1828). Excluding all such synonyms and invalid taxa, so far as we could, the database contains information on 528 species, named from 1824 to August 2007. Newly described taxa from August 2007 up to the date of submission of the present work form only an insignificantly small proportion of the total number. Therefore, their exclusion from the dataset is not likely to impact our general conclusions.

Data analysis.—Species discovery curves (Fig. 1) were plotted for all taxa, and for major clades (temnospondyls, lepospondyls) within the sample. Other clades were not plotted because the total sample sizes were too small to provide meaningful patterns. In all cases, species numbers (y-axis) are plotted against year in which the species was named, as the measure of effort (x-axis). The study was carried out exclusively at the species level in order to provide a direct comparison with other such species-level studies, and to ensure there were sufficient numbers of taxa in each sample; generic level plots would be similar, as most genera of early tetrapods consist of a single species, whereas family-level plots contained too few taxa in each bin to permit meaningful statistical analysis.

For studies of geographic and stratigraphic effects, the species were partitioned according to modern continents, listed here, with major countries that have yielded early tetrapod fossils: Africa (Madagascar, Morocco, South Africa), Asia (China, Israel, Kazakhstan, Mongolia), Australia, Europe (Czech Republic, Estonia, France, Germany, Ireland, Italy, Latvia, Norway, Poland, United Kingdom), Greenland, India (India, Pakistan), North America (Canada, USA), Russia, and South America (Argentina, Brazil, Uruguay). Species records were further binned by series (Lower and Upper Carboniferous; Lower, Middle, and Upper Permian; Lower, Middle, and Upper Triassic; Lower, Middle, and Upper Jurassic; and Lower Cretaceous). Note that we have used current stratigraphic divisions, in which for example the former "Upper Permian" is subdivided into Middle and Upper series (Gradstein et al. 2004).

In making comparisons between geographic areas and between time intervals, we distinguish raw data from corrected data. In the case of geographic regions, we did not adjust the figures for geographic area because such adjustments are many and disputed (simple land area; area of land not covered by ice; area of land not covered by forests; area of rock exposure; area of exposure of rock of different ages; area of exposure of continental rock formations), and we report results with this lack of adjustment in mind. In the case of stratigraphic series (epochs), correction is easier. Series durations are variable (5–40 million years, in our case), so we present raw diversity data, and corrected diversity data in which the raw figures are divided by series duration.

Cumulative totals per decade were plotted as histograms (Figs. 3, 5) and as curves representing proportions of the cumulative total (Figs. 4, 6). The three data series, for 1900, 1950, and 2000 were compared for similarity using the Kruskal-Wallis Test, a non-parametric ANOVA, that assesses whether all three share the same distribution or not. More specifically, the test seeks to assess equality in the medians of the samples. A further consideration of all three pairs of samples was carried out using a post-hoc non-parametric Bonferroni-type multiple comparisons.

Discovery curves may approximate many shapes. When collecting has been long-term and is reaching saturation, the curve may show its mature sigmoid (logistic) shape, with an initial slow pick-up, a phase of rapidly rising recovery of new taxa, and then a variably long phase during which the curve is an asymptote to the presumed final total. In cases where the curve is used to predict an ultimate total number of taxa, sampling has to be better than 90% complete (Bebber et al. 2007); if it is not, what looks like an asymptote may steepen with a further phase of rapid accumulation of taxa. Such unexpected late accelerations are seen in the discovery curve for dinosaurs for example, with the post-1990 burst of new taxa from China, after a long period of levelling-off from 1950 onwards (Benton 1998, 2008). In many cases, discovery curves have not yet reached the asymptote, and this suggests the probability of many further finds. In this study we use discovery curves simply as an empirical record of work so far, and as a test of sampling, not as a means to extrapolate final diversity.

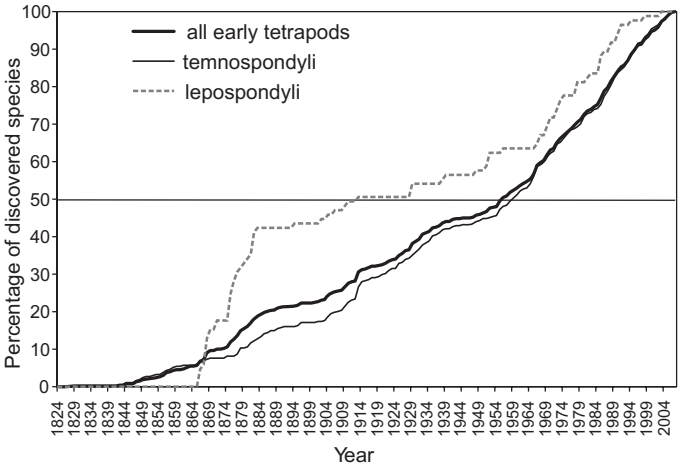

Fig. 1. Discovery curve of valid early tetrapod species (i.e., tetrapods, excluding Lissamphibia and Amniota), plotted against publication year. Species determined as synonymous or dubious in recent revisions are excluded. The curves show proportions through time, rising to 100% of current knowledge, for all early tetrapods (n = 528) and two major sub-divisions, temnospondyls (n = 368), and lepospondyls (n = 85).

doi:10.4202/app.2009.0025

Results

Discovery curves.—The discovery curve for all early tetrapods (Fig. 1) has not reached an asymptote, but approximates a somewhat concave-up curve. The initial discovery rate, from 1828 to 1850, was slow, with only ten valid species named during that interval. Accelerations in discovery rate happened about 1870 and 1950 with two relatively steep steps, one in 1913 when 13 new species were named (the most so far in a year), and another in 1966, when 12 new species were named.

Historical events had some effect, but perhaps not quite as one might have expected. The impact of the First World War (1914–1918) on publication efforts was apparently minimal, as new discoveries continued throughout the war, but only one or two new species per year were named in the four or five years after the war (Fig. 1). There was a more marked dip in species discovery before, during, and after the Second World War (1939–1945): for three years no new species were named at all, and the species discovery rate remained at one or two per year until 1955.

Different groups of early tetrapods show different patterns. Thus, the temnospondyls (Fig. 1), representing the bulk of early tetrapods (368 of 528 species; 70%), show a similar pattern up to 1964, with temnospondyl discovery lagging slightly behind all early tetrapod naming, and since then the pattern has been almost identical. The initial slow accumulation is followed by a slowly steepening discovery curve through to the present day, but with no sign of an asymptote.

The lepospondyls, on the other hand, show a more intermittent pattern of discovery (Fig. 1), partly because the overall sample size is smaller, but also perhaps because they are generally small in size, and many have been found in fossil Lagerstätten deposits, such as ancient lakes. This means that the discovery of an appropriate deposit leads to the recovery of many taxa at one time. The first species were named in the 1860s, forty years after the first early tetrapods, and the rapid jumps in numbers of valid new species reflect groups of finds in the Joggins localities in Canada and the Nýřany deposits of the Czech Republic. The discovery curve flattened off from 1880 to 1970, with a low rate of addition of taxa, and an analyst making this study in 1960 might have concluded that more or less all lepospondyls had been sampled. Since 1966, the discovery rate has increased, with restudy of older collections and the discovery of new localities. In light of periods of previous stasis, the slight levelling of the curve since 1990 has not lasted long enough to be judged an asymptote.

Growth of knowledge.—When snapshots of knowledge are taken, in 1900, 1950, and 2000, the plot (Fig. 2) can be seen to have changed shape as knowledge accumulated. In 1900, the only substantial peak was for Upper Carboniferous tetrapod species, based mainly on specimens collected during the previous century from commercially exploited coal-bearing beds in Europe and North America. By 1950, there were further modest rises in the diversities of early tetrapods in all stratigraphic series, but especially in the Lower Permian, largely because of new finds by Everett Olson, Alfred Romer, and Peter Vaughn, among others, from the red beds of the North American Midwest. The first finds from the Upper Devonian had just been made. There were further modest peaks in the 1950 data in the Lower Triassic, reflecting new finds from Russia and South Africa, and from the Upper Triassic, based on discoveries from Europe and North America, but also from South America.

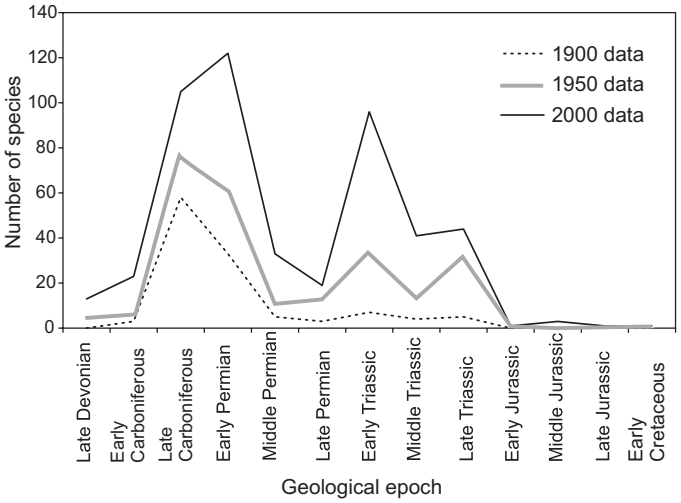

Fig. 2. Perceptions of early tetrapod diversity at three points in research time, 1900, 1950, and 2000. Total numbers of valid species are indicated per series; the 1900 data distribution differs significantly from those for 1950 and 2000, but the 1950 and 2000 distributions do not differ significantly (see text).

The following 50 years have led to substantial apparent changes in our perception of early tetrapod diversity through time. By 2000, the Lower Permian had taken over from the Upper Carboniferous as the main peak, and what might have been read as a modest recovery in diversity from the Middle to Upper Permian has reversed to suggest a continuing decline in diversity from Lower to Middle to Upper Permian. Further, a substantial new diversity peak had grown in the Lower Triassic, as a result of abundant new finds by Mikhail Shishkin, Anne Warren, Dhurjati Sengupta, and others from Russia, Australia, India, South Africa, and Madagascar. In addition, the first post-Triassic finds appear, essentially isolated records from each series of the Jurassic and from the Lower Cretaceous.

Do these changes in temporal species diversity mean that perceptions of evolutionary pattern have changed through research time? Our data suggest that they have. The null hypothesis that all three data series could have the same distribution is rejected (Kruskal-Wallis Test: corrected H value = 9.023; chi-square value = 5.991 at $p = 0.05$). Comparison of all three pairs of distributions showed that the 1900 and 1950 datasets might be the same (rank difference, 4.923), as might the 1950 and 2000 datasets (rank difference, 5.962), but the 1900 and 2000 datasets are significantly different at $p < 0.05$ (rank difference, 10.885). The null hypothesis of possible

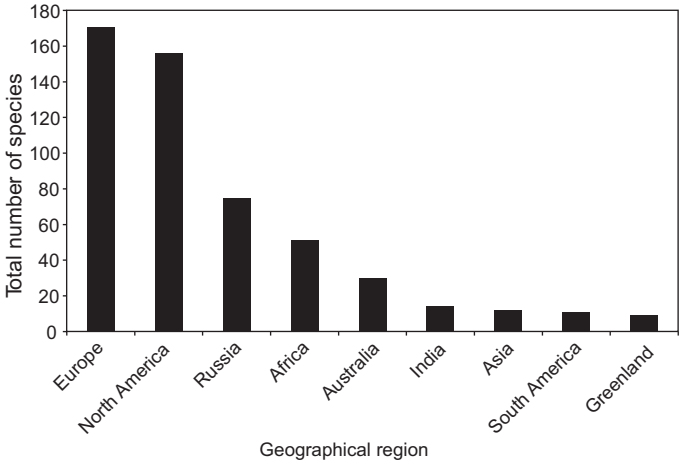

Fig. 3. Histogram of the total number of valid early tetrapod species from each major geographic region. Totals are: Europe (171), North America (156), Russia (77), Africa (51), Australia (30), India (14), Asia excluding India (12), South America (11), and Greenland (9).

identity of distributions was also rejected (Kruskal-Wallis Test: corrected H value = 4.131; chi-square value = 5.991 at $p = 0.05$) when differences among all three snapshots were compared (i.e., change from 1900 to 1950, from 1950 to 2000, and from 1900 to 2000). However, the Bonferroni-type multiple comparison did not detect significant differences between any pairs of differences between year samples (1950–1900 versus 2000–1950, rank difference 5.846; 2000–1950 versus 2000–1900, rank difference 3.077; 1950–1900 versus 2000–1900, rank difference 8.923, all at $p < 0.05$). The comparison of 1900 and 2000 came closest to significance (required rank difference of 10.677 at $p < 0.05$).

This result differs from previous studies that suggest no substantial change in overall shape of the diversity pattern with accumulating knowledge. For example, Maxwell and Benton (1990) showed that the overall patterns of tetrapod diversification had not changed substantially from 1900 to 1987, despite a doubling of numbers of known taxa. Similarly, Sepkoski (1993) reported no substantial change in diversity patterns for marine invertebrates over a ten-year period (1982 to 1992). The difference in our case arises presumably because of the smaller overall sample size (n = 528 species here, against 915 for all tetrapod families in Maxwell and Benton 1990), but more probably because the present study concerns species, and the two cited earlier studies were at family level. Species are discovered and synonymised at faster rates than families, and so their discovery patterns may appear more volatile than for families and higher taxa.

Unfortunately there is no meaningful way to extend this comparison to compare calculated rates of origination and extinction of early tetrapods through study time; nearly all the taxa here are singletons (occurring in a single stratigraphic stage) and so there is effectively 100% origination and 100% extinction at the beginning and end of each stratigraphic stage.

Sampling by geographic region.—Finds from Europe and North America dominate the plot of species numbers per modern continent (Fig. 3), accounting for 61.5% of all currently valid species of early tetrapods. Low totals from India, Australia, and Greenland might reflect the availability of appropriate rocks to some extent, but the low sample sizes from South America and Asia (excluding India) may reflect much less intensive collecting and study in those regions.

Cumulative discovery curves from each geographic region (Fig. 4) show that none of them displays any sign of reaching saturation in the near future. (Note that the Green-

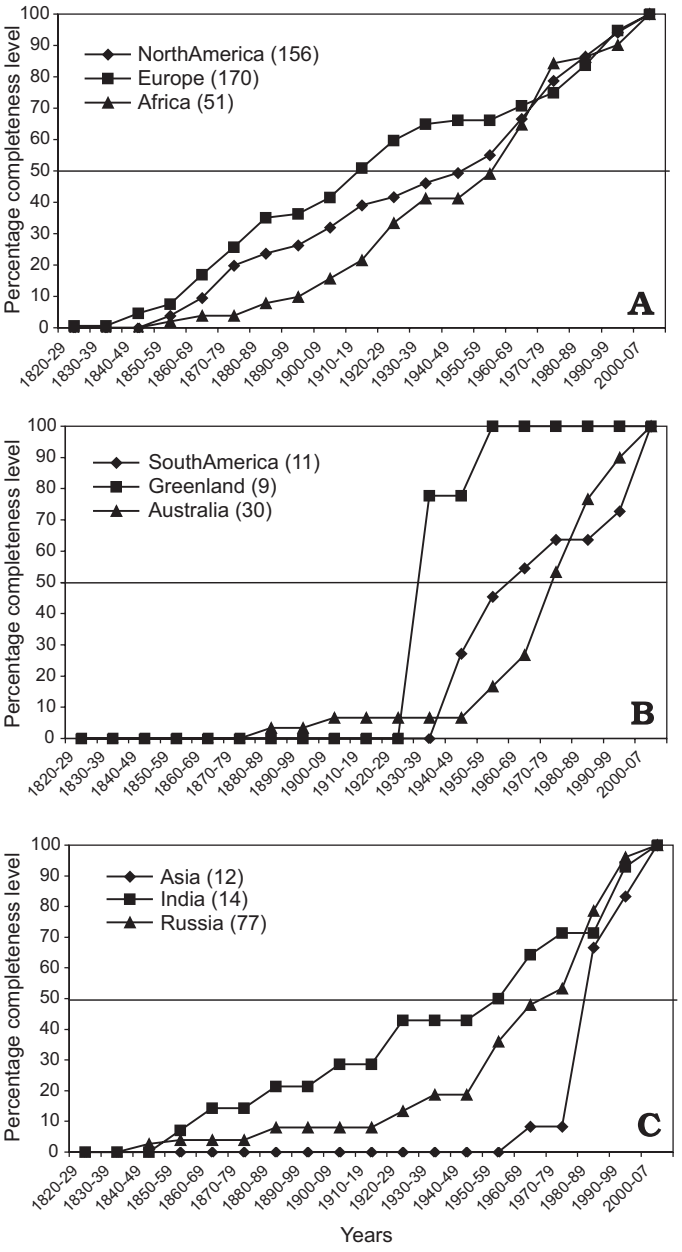

Fig. 4. Cumulative discovery curves of species of early tetrapods showing the relative completeness for each of the nine major geographic regions: North America, Europe, and Africa (**A**), South America, Greenland, and Australia (**B**), Asia, India, and Russia (**C**), plotted against decades in research time. The horizontal line marks the "half life" of the discovery curve, the date by which half the currently valid taxa had accumulated. Total numbers of taxa are given for each continent.

doi:10.4202/app.2009.0025

land curve (Fig. 4B) does reach an asymptote, but with only nine species, this curve is untrustworthy.) The starting points differ, with discoveries before 1850 recorded for Europe, North America, Africa, Russia, and India, but with much later starts in Australia (1880s), Greenland (1930s), South America (1940s), and Asia, excluding India (1960s). The two most productive continents, Europe and North America, show rather different cumulative discovery curves (Fig. 4A). The early uplift in species numbers in Europe is perhaps not surprising. Palaeontological research was already well established in Europe before 1850, and researchers, as well as the public, were as fascinated by Carboniferous and Triassic temnospondyls as with dinosaurs: when Sir Richard Owen designed the famous life-sized dinosaurs for the re-housed Great Exhibition at Crystal Palace in 1853, *Mastodonsaurus*, the "giant Triassic frog", was as startling and significant an exhibit as the dinosaurs *Megalosaurus* and *Iguanodon* (Benton and Gower 1997). Active coal mining from 1850–1900, still largely using hand tools, was another major stimulus in the recovery of relatively abundant fossils of Upper Carboniferous tetrapods on both sides of the Atlantic, with substantial numbers of new taxa described by David ("DMS") Watson in Europe and Edward Cope in North America. Overall, new species from Europe were recovered faster than from North America from the 1820s to the 1970s, when the rapidly rising trend in North America that started in the 1960s, with key workers including Alfred Romer and Robert Carroll, overtook the European curve.

The species discovery curve for Africa (Fig. 4A), with a lower global total than from Europe or North America, lags substantially behind, with a rather slow rate of accumulation of new taxa until the 1930s, when there was a jump in the total, and again in the 1950s; the cumulative total has increased comparably since the 1970s. The earliest finds resulted from sporadic colonial activity in South Africa (surveying, road building, and mining) during the nineteenth century. Expeditions from Europe to a number of African countries (or colonies) from 1900–1950 provided a small number of new species, and international collaborations since 1950 have further expanded the total.

Discovery curves from the other continents (Fig. 4B, C) are harder to interpret because of the overall low total numbers of taxa. Relatively few new taxa have been reported from Greenland since the rush of discoveries from the first expeditions in the 1920s and 1930s by Gunnar Säve-Söderbergh and Erik Jarvik (Clack 2002); many more might emerge with renewed collecting or the discovery of new localities. South America and Australia show similar patterns of species accumulation, with low rates until the 1950s, and rapid species accumulation since then. In both regions, palaeontological research prior to the mid 20th century was generally sporadic, and often linked to expeditions sent out from Europe. After 1950, locally based palaeontologists such as John Cosgriff began more systematic collecting in fossiliferous horizons, and located many new productive basins. For example, in Australia, only a few taxa had been recorded before 1950, but after that date new materials were added by a variety of workers in the 1960s and 1970s, and especially by Anne Warren and her students, who named 13 new species from Carboniferous, Permian, and Triassic localities in Australia.

India and Russia yielded their first valid taxa of early tetrapods early in the historical record, but there were relatively low rates of discovery in these areas until the 1920s, followed by several steps in accumulation rate, and rising to the present day (Fig. 4C). The story in both areas reflects government funding. In Russia, relatively few palaeontologists were active before 1940, but numbers built up through the 1960s and 1970s, with Mikhail Shishkin, Vitalii Ochev, Leonid Tatarinov, Petr Tchudinov, Nikolas Kalandadze, Andrey Sennikov, Yuri Gubin, and Igor Novikov, to name a few, particularly active, and so too did the discovery rate of new species (apparent rates are even higher than shown here, but many synonyms have not been included in our counts). After 1990, with perestroika and the decline in the central economy, valid new species of early tetrapods are rarely reported from Russia, a trend also noted for trilobites (Tarver et al. 2007), and we would expect this to be the broad pattern for all fossil groups. In India, on the other hand, with steady (if low) investment in palaeontological research, the discovery rate has remained constant. Asia excluding India (essentially China) showed the latest start in the naming of early tetrapods, followed by a steep discovery curve since the 1980s (Fig. 4C), after the Cultural Revolution and the new impetus in palaeontological research. It is unclear whether the unusually low numbers of early tetrapod species from China reflect a real absence, or perhaps the greater attention given at present to Jurassic and Cretaceous dinosaurs and birds.

We introduce here a new tool for the description and comparison of discovery curves, the "half life" date (Figs. 4, 6). This is the date, here measured as a decade, by which half of the currently valid taxa had accumulated. The species discovery half life clearly changes as the date of study advances, but it should stabilise once the asymptote of collecting is reached. However, at any point of observation, the species discovery half life gives a single numerical measure that reflects the relative maturity of collecting among analogous samples. Hence, for the geographic regions (Fig. 4), we can read off the half life of each from the 50% line, as follows: Europe (1910s), Greenland (1920s), North America (1940s), Africa, South America, and India (1950s), Russia (1960s), and Australia and Asia excluding India (1970s). Note that figures for continents other than Europe, North America, Russia, and Africa are based on rather small sample sizes ($n < 40$), so these may not be reliable.

Sampling by geological time interval.—Numbers of early tetrapod species reported from each of the series (Fig. 5A) vary substantially. Highest levels are, in sequence, in the Lower Permian, Lower Triassic, and Upper Carboniferous, with lower levels in the remaining Carboniferous, Permian, and Triassic series, and minuscule levels in the Jurassic and

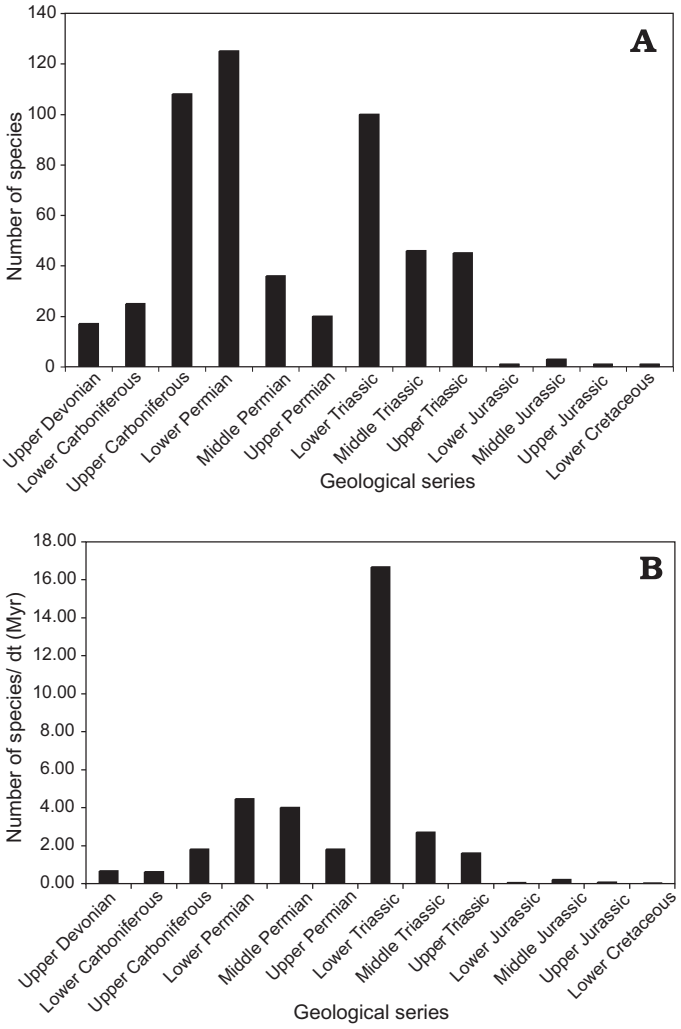

Fig. 5. Histogram of the total number of valid species discoveries of early tetrapods from each of the 13 stratigraphic series (**A**), and those figures corrected for duration, in Ma, of each series (**B**). Totals are Upper Devonian (17), Lower Carboniferous (25), Upper Carboniferous (108), Lower Permian (125), Middle Permian (36), Upper Permian (20), Lower Triassic (100), Middle Triassic (46), Upper Triassic (45), Lower Jurassic (1), Middle Jurassic (3), Upper Jurassic (1), and Lower Cretaceous (1).

Cretaceous. These variations in sample size are not all the result of differing time durations: the time-corrected diversity chart (Fig. 5B) shows that the apparently high diversities of the Lower Permian and Upper Carboniferous time bins may indeed reflect the relatively long durations of those series. Strikingly, however, the Lower Triassic, only some 3–5 Myr in duration, turns out to have the highest relative species diversity when species totals are corrected for series durations.

The species discovery curves for each series (Fig. 6) show substantial variation. In terms of a sequence from rapid early accumulation of species to later species accumulation, the Upper Carboniferous curve differs substantially from the others, reaching its half life in the 1880s (Fig. 6A), whereas the other Palaeozoic samples reached their half lives during the twentieth century: Lower Permian (1950s), Lower Carboniferous (1970s), Middle Permian (1970s), Upper Devonian (1980s). In the second set of samples (Fig. 6B), the Upper Triassic sample reached its half life first, in the 1930s, followed by the Upper Permian (1950s), Lower Triassic (1960s), and Middle Triassic (1960s). This analysis highlights the importance of the late-nineteenth century studies of the Upper Carboniferous of Europe and North America in particular, and that the Permo-Triassic red beds were not heavily studied until the twentieth century.

The recent boosts in species diversity from the Upper Devonian and Lower Carboniferous reflect dramatically increased interest in early tetrapods from both series, partly linked with intensive studies of the origin of tetrapods and

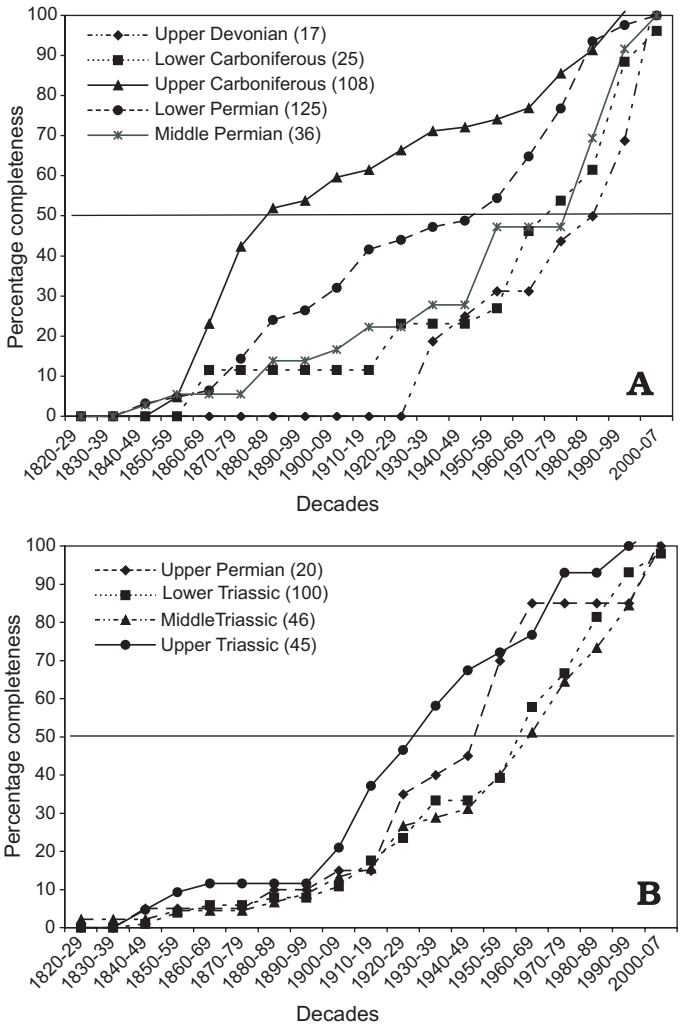

Fig. 6. Cumulative discovery curve of species of early tetrapods showing the relative completeness for each of the eight stratigraphic series, divided into two panels, from Upper Devonian to Middle Permian (**A**), and Upper Permian to Upper Triassic (**B**), plotted against decades in research time. The horizontal line marks the "half life" of the discovery curve, the date by which half the currently valid taxa had accumulated. Numbers of taxa per series are: Upper Devonian (17), Lower Carboniferous (25), Upper Carboniferous (108), Lower Permian (125), Middle Permian (36), Upper Permian (20), Lower Triassic (100), Middle Triassic (46), Upper Triassic (5), Jurassic (5), Cretaceous (1).

doi:10.4202/app.2009.0025

the fin-to-limb transition (Clack, 2002), as well as investigations of the substantial hiatus in the record of early tetrapods through the Lower Carboniferous, the so-called "Romer's gap" (Clack 2002) of some 20 Myr. This "gap" has now been partially filled by discoveries of new localities, such as Dumbarton in Scotland, and others on both sides of the Atlantic (Clack 2002; Ward et al. 2006).

Discussion

Discovery curves for fossil taxa.—The shapes of discovery curves likely depend on a number of factors. They would be expected to reflect the chosen taxonomic level; that is, new higher taxa, such as orders or families, ought to accumulate earlier than lower taxa, such as genera and species. Indeed, this is the case for trilobites (Tarver et al. 2007), where the discovery curves for genera, families, superfamilies, suborders, and orders become progressively more convex upwards. All nine currently recognised orders of trilobites had been discovered (but not necessarily named) by 1840, all 17 suborders by 1870, all 32 superfamilies by 1970, and all 179 families by 1990. In comparing from group to group, then, one should compare plots at similar, ideally identical, taxonomic levels.

Early tetrapods show no evidence for an asymptote in their species discovery curves, whether for the whole sample or for certain clades within that sample (Fig. 1), or for geographic (Fig. 4) or temporal (Fig. 6) partitions. For the whole sample, the discovery curve is slightly concave, with a modest increase in slope after 1960. This indicates steady activity over the years, bearing in mind that the identification and removal of synonyms and dubious taxa is more likely to be more complete for the earlier phases of the record than for the past twenty or thirty years (Alroy 2002). Indeed, the post-1960 steepening of the slope could result from undetected synonyms and dubious taxa that may be identified and removed in future studies.

The slightly concave pattern for the species discovery curve of early tetrapods is not necessarily the only possible shape. One might expect a variety of curve types, ranging from more deeply concave, through linear, to sigmoid, perhaps reflecting the completeness of sampling efforts. The fully developed sigmoid curve, with an initial period of slow reporting of new species, followed by a rush of new valid taxa, and then a slowing down, might be observed for a group that has been well sampled, such as modern birds or mammals (Benton 1998; Bebber et al. 2007). A concave-up curve, reflecting a long "slow" period with a recent acceleration in study might then represent a rather poorly sampled group. A more or less linear species discovery curve, as seems to be the case for many modern groups such as New World grasses and ferns (Bebber et al. 2007), might indicate steady work and no episode of unusually intensive study. The curves are unlikely to reflect fossil record quality alone; a deeply concave-up curve might indicate no more than a lack of interest in studying that group until recently.

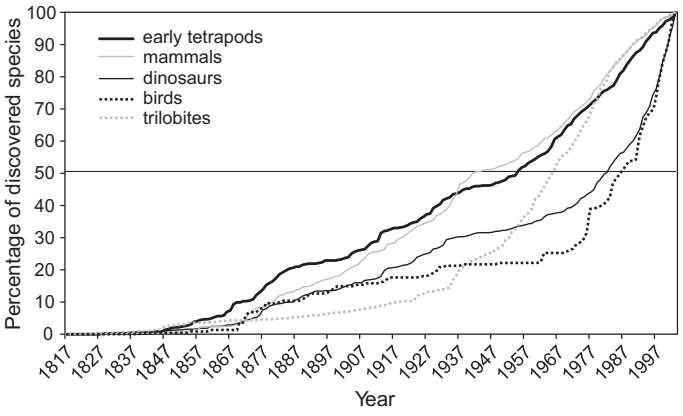

Fig. 7. Species discovery curves for several groups of fossil organisms show substantial differences in form. All discovery curves are shown as percentages, even though final totals, in 2003, are very different: trilobites (n = 4126), early tetrapods (n = 515), dinosaurs (n = 694), fossil birds (n = 221), and fossil mammals of North America (n = 3340). The horizontal line marks the "half life" of the discovery curve, the date by which half the currently valid taxa had accumulated. Data from these sources: trilobites (Tarver et al. 2007), dinosaurs (Benton 2008), fossil birds (Fountaine et al. 2008), fossil mammals (Alroy 2002).

Linear and concave species discovery curves are seen among fossil taxa (Fig. 7). The discovery curves for early tetrapods and mammals track each other very closely, both approximating a straight line. Then, in order of depth of concavity, come trilobites, dinosaurs, and birds. This is exemplified by the 'half life' measurements, where 50% of the current total was achieved as follows: mammals (1940s), early tetrapods (1950s), trilobites (1960s), dinosaurs (1980s), and birds (1990s). The curve for fossil birds is deeply concave because of a substantial increase in species discovery since 1970, triggered especially by the discovery of abundant new taxa in the Lower Cretaceous of Liaoning Province, China, and by the arrival of new palaeornithologists on the scene who have expanded the Palaeogene record in particular. Note that only the trilobite and fossil mammal curves may be seen as reliable, in that the others are based on rather smaller sample sizes.

The issue of reliability is confirmed in a comparison of dinosaur species discovery curves compiled ten years apart (Benton 1998, 2008). The discovery curve for dinosaur species (n = 300) presented by Benton (1998) showed much earlier activity, with the 20% level reached about 1860, and the 50% level by 1885. Current figures (Benton 2008), as we have seen, yield 20% and 50% levels at about 1920 and 1985, respectively (Fig. 7). The post-1985 explosion in publications of new dinosaur taxa from less explored territories such as China and South America, as well as from well-sampled areas such as North America, may be exaggerated by undetected redundancy (synonymy, nomina dubia), but part of that increase, following an apparent asymptote in the 1980s (Benton 1998), is evidence that calculations of ultimate totals from discovery curves are likely to be unreliable unless sam-

pling is nearly complete (Bebber et al. 2007), and that can hardly be demonstrated in real examples.

The pattern of a discovery curve may reflect the real rate of recovery of new taxa against constant effort by palaeontologists, or it could represent varying degrees of effort in searching over the same ground. In previous studies where worker effort has been quantified (e.g.,Wickström and Donoghue 2005; Tarver et al. 2007), recent rises in discovery rate are likely linked to vastly increased collector effort, whether measured by numbers of active workers or numbers of published papers. However, the evidence is that worker effort has been increasing rapidly since the 1960s, with many more professional palaeontologists active worldwide, and many more papers published; yet, these increased efforts do not map onto an arithmetical increase in species discovery. The present study provides an excellent case in point: a search on Web of Science© (search was "temnospondyl OR labyrinthodont") reveals a rise in numbers of recorded papers on early tetrapods from four in the decade 1970–9, to ten (1980–9), 39 (1990–9), and 110 (2000–8). This rise is almost certainly not entirely real—Web of Science© did not sample palaeontological journals well until the 1990s, and the search terms retrieve review papers and non-systematic studies (some 10% of the total). The results though give an indication of a clear increase in the overall number of publications, but without a marked increase in the discovery of new taxa. In fact, the discovery curve for the past decades may be too steep, enhanced by so-far undetected synonymous and dubious taxa that are yet to be deleted.

Changes in rates of species description can move up or down according to systematic philosophy or fashion of course. There has always been a tension between "splitting" and "lumping", where some workers divide species more finely (splitters) than others who prefer to encompass a considerable amount of individual variation in a single species (lumpers). Further, for living organisms at least, new methods in molecular biology have revealed previously cryptic species. In the case of the species discovery curves here (Fig. 7), the assessment of validity of species is based on current work, and is not a reflection of former opinions, the distinction between "now" and "then" interpretations of validity (Alroy 2002), so any move to excessive splitting or lumping in the past decade of research would affect our current perception of the whole species discovery curve.

Worker effort and macroevolutionary patterns.—A key aim of this study was to determine how human factors might have affected our perceptions of early tetrapod evolution. In particular, can we detect any of the usually expected biases in the fossil record?

Sampling bias: apparent diversity of a fossil group might simply reflect sampling effort or rock availability, or both (Raup 1972; Alroy et al. 2001; Peters and Foote 2001, 2002; Smith 2001, 2007).

Age-related sampling bias: older stratigraphic levels might well be less well sampled than more recent (Raup 1972).

Post-extinction hiatus: certain mass extinction horizons are associated with worldwide marine regressions, and this tends to remove the post-extinction marine fossil record (Smith 2001, 2007).

We do not present a detailed study here of the overall issue of sampling, as this requires estimation of rock area and rock volume to determine rock availability: such studies are underway. However, the effects of worker effort on variations in time-corrected species numbers per series provide some insight into sampling through geological time (Fig. 4B). This has some bearing on the broader question of sampling heterogeneity, but particularly on any age-related biases and on post-extinction hiatuses.

Global species diversities (n) of early tetrapods vary substantially through the time intervals under study: Devonian (16), Carboniferous (134), Permian (196), Triassic (180), Jurassic (5), and Cretaceous (1). When corrected for temporal duration (t), these figures (n/t) still show variation (ignoring the Devonian, Jurassic, and Cretaceous figures): Carboniferous (6), Permian (10.5), Triassic (21), and perhaps at this level one could argue that the increase represents an improvement of sampling, or at least an increase in worker effort, through geological time. There is, however, no evidence that the increases are driven simply by more active study towards the present day. Three searches on Web of Science© using the search strings "temnospondyl OR labyrinthodont and carbonif*/ perm*/ trias*" showed approximately equivalent numbers of publications from 1970–2008 on early tetrapods from each geological period: Carboniferous (145), Permian (147), Triassic (153). Palaeontologists now tend to focus on major phylogenetic questions, and these researchers are rarely limited to one country or one stratigraphic level. Any increase in worker effort through geological time is apparently not reflected in the numbers of publications. Further, the dramatic decline in temnospondyl diversity through the Jurassic and Cretaceous, geological periods that reveal abundant terrestrial tetrapods of other kinds, is probably real, and quite counter to the expectations of an improvement in study efforts toward the present.

The finer-scale analyses of species numbers at series level (Fig. 5A, B) address the questions of the changes in worker effort through geological time and post-extinction hiatuses. These data refute the simple notion of increasing diversity through geological time: the time-corrected (n/t) figures of species diversity by series are arranged non-temporally: Lower Triassic (17), Upper Permian (7), Upper Carboniferous (5), Lower Permian (3.5), Middle Triassic (2.5), Upper Triassic (1.5), Lower Carboniferous (1).

The two series with highest corrected diversity values are the Lower Triassic and the Upper Permian, conveniently bracketing the end-Permian mass extinction. These figures confirm a phenomenon noted by Benton et al. (2004) in their study of the Russian data, that the Lower Triassic tetrapod record is unusually well sampled, and dominated to an astonishing degree by amphibians. The main regions in which the Upper Permian and Lower Triassic fossil record of early

doi:10.4202/app.2009.0025

tetrapods is sampled are South Africa and Russia (numerous basins and successions in each) and both show no decrease in the numbers of fossiliferous localities yielding tetrapod fossils in the lowest Triassic: indeed, in the Orenburg region in Russia, the numbers of fossiliferous localities increase across the Permo-Triassic boundary. There is no evidence for a post-extinction hiatus in sedimentation, number of fossiliferous localities, or early tetrapod diversity.

Further, the species discovery curves for the Upper Permian and Lower Triassic (Fig. 6B) show similar patterns, with, if anything, evidence for historically earlier and more rapid accumulation of new taxon records in the Upper Permian than in the Lower Triassic. These data lend no support to the idea that the end-Permian mass extinction among tetrapods could be largely or mainly an artefact of poor sampling after the event.

Conclusions

As expected, our data reveal changes in the pace of discovery of early tetrapod species through time, and these match historical contingencies. Declines during and following the world wars reflect economic imperatives at those times, and recent increases in the discovery rate must reflect at least in part the increase in investment in palaeontological research worldwide since the 1960s. Some of the increase doubtless reflects as yet undetected synonyms.

Further, as expected, the discovery curve for Europe dominated overall patterns through much of the nineteenth century, with discovery rates from North America not matching those for dinosaurs (there was no late-nineteenth century "bone rush" for early tetrapods). Other territories, such as Russia, Africa, and India have shown increasing species discovery rates in the past 50 years, and Australia, South America, and China still probably have the greatest potential for discovery of new species.

It is obvious from the discovery curves that none of the groups of early tetrapods investigated here is close to reaching saturation in recognised species diversity, and that continuing collection in all geographic and stratigraphic localities should continue. As expected, finds from both Europe and North America dominate the number of discoveries, in contrast to countries such as Africa and South America that have been poorly sampled. Continuing worker effort in Africa, India, South America, and Australia should see further rises in their discovery curves.

This study does not find evidence that collecting and publication effort has driven apparent diversity of early tetrapods through time, but further standardisation against rock availability is still required. Temporal patterns of diversity are apparently not a result simply of increasing worker effort from late Palaeozoic to Mesozoic samples. Further, sampling appears to improve across the Permo-Triassic boundary, so it would be hard to make a case that the massive extinction of tetrapod taxa at the end of the Permian was simply, or even substantially, an artefact of sampling.

Acknowledgements

We thank Rich Cifelli (University of Oklahoma, Norman, USA), as editor, and referees Linda Wickström (Swedish Geological Survey, Stockholm, Sweden) and Mark Wilkinson (Natural History Museum, London, UK) for very helpful comments on the MS. Parts of this paper are taken from EB's MSc project. We thank Gareth Dyke (University College, Dublin, Ireland) for the fossil bird data, and John Alroy for the fossil mammal data, used in Fig. 7. MJB and MR are grateful for funding from NERC grants NE/C518973/1 and NE/F014872/1. JET is funded by NERC grant NER/S/A/2003/11198A.

References

Alroy, J. 2002. How many named species are valid? *Proceedings of the National Academy of Sciences, USA* 99: 3706–3711. http://dx.doi.org/10.1073/pnas.062691099

Alroy, J., Marshall, C.R, Bambach, R.K., Bezusko, K., Foote, M., Füürsich, F.T., Hansen, T.A., Holland, S.M., Ivany, L.C., Jablonski, D., Jacobs, D.K., Jones, D.C., Kosnik, M.A., Lidgard, S., Low, S., Miller, A.I., Novack-Gottshall, P.M., Olszewski, T.D., Patzkowsky, M.E., Raup, D.M., Roy, K., Sepkoski, J.J. Jr., Sommers, M.G., Wagner, P.J., and Webber A. 2001. Effects of sampling standardization on estimates of Phanerozoic marine diversification. *Proceedings of the National Academy of Sciences, USA* 98: 6261–6266.

Bebber, D.F., Marriott, F.H.C., Gaston, K.J., Harris, S.A., and Scotland, R.W. 2007. Predicting unknown species numbers using discovery curves. *Proceedings of the Royal Society of London, Series B* 274: 1651–1658. http://dx.doi.org/10.1098/rspb.2007.0464

Benton, M.J. 1985. Mass extinction among non-marine tetrapods. *Nature* 316: 811–814. http://dx.doi.org/10.1038/316811a0

Benton, M.J. 1996. Testing the roles of competition and expansion in tetrapod evolution. *Proceedings of the Royal Society of London, Series B* 263: 641–646. http://dx.doi.org/10.1098/rspb.1996.0096

Benton, M.J. 1998. The quality of the fossil record of vertebrates. *In*: S.K. Donovan and C.R.C. Paul (eds.), *The Adequacy of the Fossil Record*, 269–303. Wiley, New York.

Benton, M.J. 2008. How to find a dinosaur, and the role of synonymy in biodiversity studies. *Paleobiology* 34: 516–533. http://dx.doi.org/10.1666/06077.1

Benton, M.J. and Gower, D.J. 1997. Richard Owen's giant Triassic frogs: archosaurs from the Middle Triassic of England. *Journal of Vertebrate Paleontology* 17: 74–88.

Benton, M.J. and Simms, M.J. 1995. Testing the marine and continental fossil records. *Geology* 23: 601–604. http://dx.doi.org/10.1130/0091-7613(1995)023%3C0601:TTMACF%3E2.3.CO;2

Benton, M.J. and Storrs, G.W. 1994. Testing the quality of the fossil record: paleontological knowledge is improving. *Geology* 22: 111–114. http://dx.doi.org/10.1130/0091-7613(1994)022%3C0111:TTQOTF%3E2.3.CO;2

Benton, M.J., Wills, M.A., and Hitchin, R. 2000. Quality of the fossil record through time. *Nature* 403: 534–537. http://dx.doi.org/10.1038/35000558

Benton, M.J., Tverdokhlebov, V.P., and Surkov, M.V. 2004. Ecosystem remodelling among vertebrates at the Permian–Triassic boundary in Russia. *Nature* 432, 97–100.

Cain, S.A. 1938. The species-area curve. *American Midland Naturalist* 19: 573–581. http://dx.doi.org/10.2307/2420468

Carroll, R.L., Bossy, K.A., Milner, A.C., Andrews, S.M., and Wellstead, C.F. 1998. *Handbuch der Paläoherpetologie: Teil 1, Lepospondyli*. 216 pp. Dr. Friedrich Pfeil, Munich.

Clack, J.A. 2002. *Gaining Ground: the Origin and Early Evolution of Tetrapods*. 369 pp. Indiana University Press, Bloomington.

Fara, E. 2002. Sea-level variations and the quality of the continental fossil record. *Journal of the Geological Society* 159: 489–491.

Fara, E. and Benton, M.J. 2000. The fossil record of Cretaceous tetrapods. *Palaios* 15: 161–165.

Flessa, K.W. 1990. The "facts" of mass extinction. *Geological Society of America Special Paper* 247: 1–7.

Fountaine, T.M.R., Benton, M.J., Dyke, G.J., and Nudds, R.L. 2005. The quality of the fossil record of Mesozoic birds. *Proceedings of the Royal Society of London, Series B* 272: 289–294. http://dx.doi.org/10.1098/rspb.2004.2923

Gaidet, N., Fritz, H., Messad, S., Mutake, S., and Le Bel, S. 2005. Measuring species diversity while counting large mammals: comparison of methods using species accumulation curves. *African Journal of Ecology* 43: 56–63. http://dx.doi.org/10.1111/j.1365-2028.2004.00545.x

Gradstein, F.M., Ogg, J.G., and Smith, A.G. 2004. *A Geologic Time Scale 2004*. 589 pp. Cambridge University Press, Cambridge.

Holland, S.M. and Patzkowsky, M.E. 1999. Models for simulating the fossil record. *Geology* 27: 491–494.

Jablonski, D. 1991. Extinctions: a paleontological perspective. *Science* 253: 754–756. http://dx.doi.org/10.1126/science.253.5021.754

Jaeger, G. F. 1824. *De Ichthyosauri sive Proteosauri Fossilis Speciminibus in Agro Bollensi in Würtembergia Repertis*. 14 pp. Cottae, Stuttgart.

Jaeger, G.F. 1828. *Üeber die fossile Reptilien, welche in Württemberg aufgefunden worden sind*. 48 pp. J.B. Metzler, Stuttgart.

Maxwell, W.D. and Benton, M.J. 1990. Historical tests of the absolute completeness of the fossil record of tetrapods. *Paleobiology* 16: 322–335.

Moser, M. and Schoch, R. 2007. Revision of the type material and nomenclature of *Mastodonsaurus giganteus* (Jaeger) (Temnospondyli) from the Middle Triassic of Germany. *Palaeontology* 50: 1245–1266. http://dx.doi.org/10.1111/j.1475-4983.2007.00705.x

Norell, M.A. and Novacek, M.A. 1992. The fossil record and evolution: comparing cladistic and paleontologic evidence for vertebrate history. *Science* 255: 1690–1693. http://dx.doi.org/10.1126/science.255.5052.1690

Peters, S.E. and Foote, M. 2001. Biodiversity in the Phanerozoic: a reinterpretation. *Paleobiology* 27: 583–601. http://dx.doi.org/10.1666/0094-8373(2001)027%3C0583:BITPAR%3E2.0.CO;2

Peters, S.E. and Foote, M. 2002. Determinants of extinction in the fossil record. *Nature* 416: 420–424. http://dx.doi.org/10.1038/416420a

Raup, D.M. 1972. Taxonomic diversity during the Phanerozoic. *Science* 177: 1065–1071.

Raup, D.M. 1979. Biases in the fossil record of species and genera. *Bulletin of the Carnegie Museum of Natural History* 13: 85–91.

Ruta, M., Coates, M.I., and Quicke, D.L.J. 2003. Early tetrapod relationships revisited. *Biological Reviews* 78: 251–345. http://dx.doi.org/10.1017/S1464793102006103

Schoch, R.R. and Milner, A.R. 2000. *Handbuch der Paläoherpetologie: Teil 3B, Stereospondyli*. 203 pp. Dr. Friedrich Pfeil, Munich.

Sepkoski, J.J., Jr. 1993. Ten years in the library: new data confirm paleontological patterns. *Paleobiology* 19: 43–51.

Smith, A.B. 2001. Large-scale heterogeneity of the fossil record, implications for Phanerozoic biodiversity studies. *Philosophical Transactions of the Royal Society, Series B* 356: 1–17.

Smith, A.B. 2007. Marine diversity through the Phanerozoic: problems and prospects. *Journal of the Geological Society* 164: 731–745. http://dx.doi.org/10.1144/0016/76492006-184

Tarver, J.E., Braddy, S.J., and Benton, M.J. 2007. The effects of sampling bias on Palaeozoic faunas and implications for macroevolutionary studies. *Palaeontology* 50: 177–184. http://dx.doi.org/10.1111/j.1475-4983.2006.00618.x

Valentine, J.W. 1969. Patterns of taxonomic and ecological structure of the shelf benthos during Phanerozoic time. *Palaeontology* 12: 684–709.

Ward, P., Labandeira, C., Laurin, M., and Berner, R.A. 2006. Confirmation of Romer's Gap as a low oxygen interval constraining the timing of initial arthropod and vertebrate terrestrialization. *Proceedings of the National Academy of Sciences, USA* 103: 16818–16822. http://dx.doi.org/10.1073/pnas.0607824103

Wickström, L.M. and Donoghue, P.C.J. 2005. Cladograms, phylogenies and the veracity of the conodont fossil record. *Special Papers in Palaeontology* 73: 185–218.

doi:10.4202/app.2009.0025